EYESTALK REGULATION OF MOLT AND VITELLOGENESIS IN *UCA PUGILATOR*

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Fiddler crabs of the species *Uca pugilator* have the most extensive continuous geographic range of the several species of *Uca* to be found in the United States. From the northern limit of their range, Cape God, Massachusetts, they occur along the east coast to the tip of Florida, along the west coast of Florida, and extend westward on the Gulf coast to Texas (Crane, 1975). Crabs of the genus *Uca* reproduce throughout the year in the tropics, but in temperate regions the breeding season is restricted to a much shorter period. Crane (1975) reported a breeding season of about two months (end of May to early August) for *U. pugilator* on Cape Cod. Salmon and Astaides (1968) reported field observations of courtship activity at Beaufort, North Carolina, where crabs were seen on the beach in early March, but courtship activity was first observed in early April and continued until late August. Herrnkind (1968) stated that approximately 10% of females in burrows were eggbearing in April, and from May to October nearly all females were ovigerous. These latter observations were presumably made near Miami, Florida. Thus, it would appear that northern extension of the range of this species is accompanied by increasing restriction of the breeding season.

Adiyodi and Adiyodi (1970, 1974) have emphasized the generally antagonistic relationship between reproduction and molting. In addition to a regulatory system channeling stored materials either into somatic growth or vitellogenesis, inhibition of molt during egg incubation is required in female decapods. The basic pattern of hormonal regulation of molt has been extensively studied and involves a molt inhibiting hormone (MIH) produced by the X-organ-sinus gland complex and a molting hormone (MH) produced by the Y-organs (Passano, 1960). The hormonal regulation of reproduction is less well understood and the interrelations between molt and reproduction still less so.

Among brachyurans that have been studied, it is not uncommon to find species that spawn more than once in an intermolt. Gomez and Nayar (1965) studied *Paratelphusa hydrodromous*, which has a breeding season restricted to the months March to September. Up to three spawnings occur within a single intermolt, and there is usually a single molt per year. Each vitellogenesis appears to occur in two phases, an initial slow phase, and a terminal rapid one, culminating in oviposition. Adiyodi (=Gomez) (1968) reported that unilateral eyestalk removal does not stimulate ovarian development in December (prior to vitellogenesis) but does stimulate it during January when slow vitellogenesis is occurring. Implants of thoracic ganglia or brain stimulate ovarian maturation during slow vitellogenesis. An ovary stimulating hormone (OSH) is postulated to be produced in the central nervous system.

Ryan (1965) described the pattern for *Portunus sanguinolentus* as nonseasonal both for molt and spawning, but with a relatively fixed interval (about 60 days)

between molt and first spawning. Thereafter, the intervals between spawnings, of which there are two more in the same intermolt, are 30 to 40 days each.

Cheung (1969) reported on the molting and spawning pattern for *Menippe mercenaria*. The study involved animals maintained in the laboratory for periods of more than a year as well as freshly collected crabs. Cheung noted that there appeared to be no difference between the two categories with respect to molt or spawning. Spawning was seasonal, peaking in August and September, dropping rapidly in October and remaining very low from November through April. Molts occurred less frequently than spawnings and with less regularity. About half occurred between November and January 31 and thus coincided with low frequency of spawning. However, the other half of the molts were scattered irregularly through the rest of the year. This crab spawns several times in one intermolt with apparently no fixed intervals between molt and first spawning or between subsequent spawnings. Cheung also studied the effect of destalking at various times of year. The results were somewhat ambiguous: molt alone was induced in ovigerous crabs destalked at the end of August and in nonovigers destalked in November; during these same times, molt followed by one or more spawnings was also induced by the operation. Crabs destalked in March when controls molted had the molt accelerated. Spawning alone (*i.e.*, not preceded by molt) occurred in practically all of a group destalked in mid-September, and there were no intact controls for this experiment. Cheung concluded that a number of factors operate to modify the results of destalking, including light, temperature, and salinity.

Bomirski and Klek (1974) described reproduction in *Rhithropanopeus harrisii* in which spawning is restricted to June through August. The reproductive season ends with a molt, following which vitellogenesis proceeds at a slow rate through the winter, reaching completion at first spawning of the next year. In the early part of the breeding season, vitellogenesis accompanies incubation of eggs, and spawning immediately follows hatching. In the latter half of the season no vitellogenesis occurs until after the ecdysis that terminates the season. During the slow vitellogenesis in autumn, destalking stimulates ovarian development; during rapid vitellogenesis in summer and during the resting period in late summer, destalking produces little, if any, stimulation.

Brown and Jones (1949) showed that removal of eyestalks from *Uca pugilator* induced ovarian growth and that implantation of sinus glands prevented such growth in destalked crabs. Their experiments were carried out between July 10 and August 12 at Woods Hole, Massachusetts, and therefore would have been in the latter part of the breeding season, as reported by Crane. Brown and Jones found that only 7 out of 31 controls showed mature ovaries as judged by color, and that no controls laid eggs during the experimental period. They do not mention any molts that may have occurred. Guyselman (1953), also working at Woods Hole, reported destalking females on July 28; all molted between 5 and 21 days after destalking. He noted that molting in the controls was of very low frequency during the study. Abramowitz and Abramowitz (1940) reported destalking *Uca pugilator* during the summer at Woods Hole and thereby stimulating molt. They also stated that the crabs breed in September. However, there is some question about the immediate relevance of this report, since both the photographs and the description suggest that they were using *U. pugnax* rather than *U. pugilator*.

As Bomirski and Klek (1974) have pointed out, because the response of female

crabs to eyestalk removal may vary with the species, age, and time of year, experiments on the role of OSH must be coupled with examination of the reproductive cycle. In addition, since the interrelations of molting and reproduction also vary from species to species, the molting cycle must be considered in any study of reproduction.

This study deals with ovarian development and ecdysis in intact crabs and the response to eyestalk removal during the period from September through May for *U. pugilator* from Florida.

MATERIALS AND METHODS

The crabs used in these experiments were obtained from the Gulf Specimen Co., Panacea, Florida. Shipments were received on the following dates: January 13, February 25, April 15, September 15, October 27, and December 31, 1976. The shipments of September, October, and April consisted of freshly collected crabs. The other shipments were of crabs that had been kept in holding tanks from early to mid-November. The holding tanks contained three to four feet of sand in which the crabs made burrows, and the water supply was the local sea water. After arrival at Towson, Maryland, control and experimental crabs were kept in transparent plastic containers with a small amount of artificial sea water (Instant Ocean). Food (pieces of lettuce or spinach) was placed in the containers two to three times a week, at which time the water was changed. During experimental periods crabs were examined daily for ecdysis, and when the first molt occurred, all crabs were isolated and maintained in small finger bowls until they were sacrificed.

Eyestalks were removed by cutting through the flexible membrane at the base, using a scalpel and without cautery. Illumination conditions of three kinds were used: natural illumination (with uncontrolled temperature), constant illumination, and 10L:14D. For the latter two conditions the light intensity was about 40 ft.-c, and temperature was constant at $23°$ C. Since the effects of photoperiod, if any, were very small compared with the effects of destalking for the processes discussed in this report, the results from all photoperiods are combined. In all periods, at least two of the illumination conditions were studied simultaneously.

The period of observation varied from a maximum of 30 days to 12–15 days, the shorter periods being made necessary when there was a high incidence of mortality. In general mortality was low ($< 10\%$) and occurred within 24 hours of eyestalk removal, in which case death was attributed to the surgical procedure. The experimental design called for examination of ovaries at 10, 20, and 30 days. However, when animals died, they were autopsied, and matching controls were sacrificed. All ovarian weights obtained eight days or more after destalking are included in this report.

Carapace width (CW) and weight of experimental and control crabs were recorded just prior to dissections. The carapace was removed and, on the stage of the dissecting microscope, the ovaries were dissected out and placed in sea water. Any extra-ovarian tissue was removed, and the ovaries were transferred to a previously tared plastic weighing dish. Excess water was blotted up with filter paper and the ovaries were weighed on a Mettler analytical balance. Weights were recorded to the nearest tenth of a milligram. A record was made of the color of the ovaries.
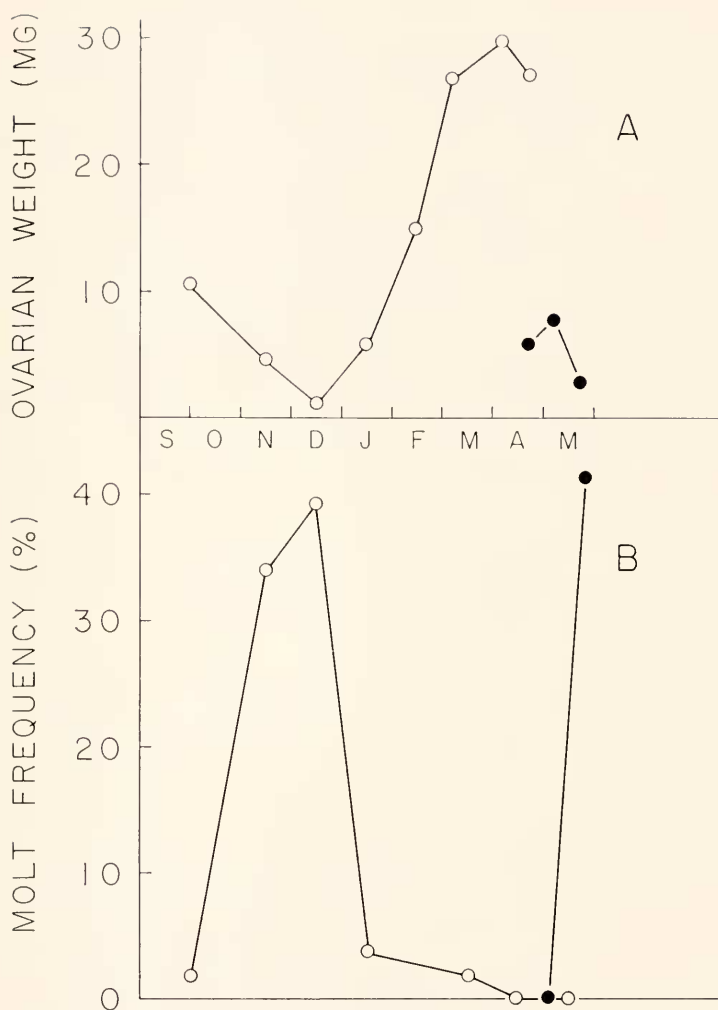
FIGURE 1. Mean ovarian weights (A) and frequency of molt (B) for intact crabs as a function of time of year. Open circles represent nonovigers; solid circles, April ovigers.

For most experiments the animals used were between 14 and 16 mm CW. In a few experiments some crabs were included that were up to 19 mm or as small as 12 mm CW. In no case, however, did the mean CW for any group exceed 16 mm or fall below 14 mm.

RESULTS

Intact crabs

The mean ovarian weights for control crabs in each of the experimental periods are presented in Figure 1A. Although, for reasons that will become obvious, it

would not be appropriate to ascribe standard errors of the mean to some points, the curve as a whole indicates a systematic change throughout the year. Ovarian weights decrease from September through December. They begin to increase in January, are well advanced in March, and when egg-laying occurs in a part of the population in April, a considerable decrease in mean weights would be recorded if the crabs were treated as a single population. Approximately 30% of the crabs received April 15 were ovigerous on arrival or laid eggs within the next week. In the rest of the population at that time, 50 to 60% had ovaries that weighed less than 30 mg, thus being below the weights at which egg-laying would be expected to occur. The crabs that were ovigerous in April did not mature another set of eggs during the next month and a half. As will be discussed later, there is evidence that these post-ovigerous crabs undergo molt prior to any further reproductive activity.

Gonadal indices (percentage of wet body weight represented by ovaries) for the experimental periods, together with the variance, number of animals used, and mean CW, are presented in Table I. The gonadal index, like the ovarian weight, reaches a minimum in December and thereafter increases to maximal values in March and April. Mean CW for control crabs ranges from 14.0 mm in December to 15.6 mm in February.

The relative frequency distributions in ovarian weight classes for four groups of crabs are shown in Figure 2A and B. The distributions in Figure 2A are for crabs received February 25, and for nonovigerous crabs received April 15. Both groups represent crabs with near maximum ovarian weights and gonadal indices. There is no single class with as much as 30% of the total number examined, and each of the three to four smallest weight classes contain about the same frequencies. The occupied classes extend up to 130–139.9 mg. Neither of the distributions in Figure 2A represents a "normal" distribution; they obviously come from a highly heterogeneous assemblage to which the application of conventional statistics is not meaningful.

The distributions in Figure 2B, for crabs received January 13 and for the ovigerous crabs received April 15, are quite different. These distributions are characterized by a high frequency in the smallest weight class (0 to 9.9 mg), a rapid drop

TABLE I

Gonadal indices (percentage of wet body weight represented by ovaries), variance (s^2), number of animals used (N) and mean carapace width (CW) for the experimental periods.

|	Destalked				Intact			
	Gonadal index	s^2	N	CW	Gonadal index	s^2	N	CW
September-October	0.94	0.242	33	14.6	0.30	0.015	41	14.6
November	1.17	0.508	22	15.9	0.35	0.036	22	15.0
December	0.481	0.048	14	14.6	0.186	0.022	14	14.0
January	2.85	4.24	31	16.0	0.471	0.10	29	14.6
February	1.62	0.397	13	15.4	0.99	0.518	16	15.6
March	3.22	4.41	51	15.3	2.00	4.202	50	15.3
April (nonovigers)					2.25	1.661	13	15.2
April (ovigers)	1.29	0.58	21	15.6	0.54	0.053	21	15.3
May (post-ovigers)	1.00	0.575	16	15.6	0.438	0.066	16	15.3
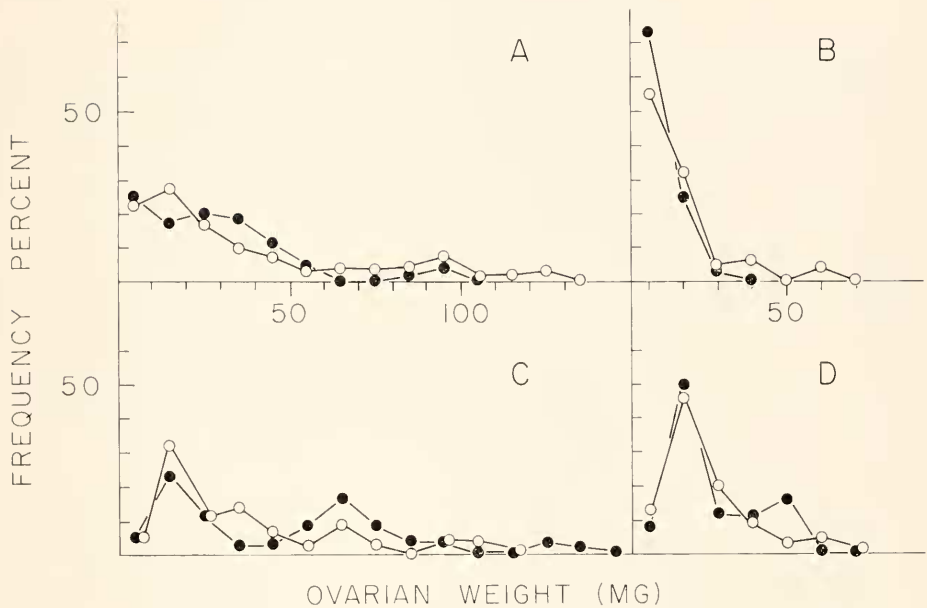
FIGURE 2. Frequency distributions by weight classes for crab ovaries: A, open circles, controls from February 25 shipment; solid circles, nonovigerous controls from April 15 shipment; B, open circles controls from January 13 shipment; solid circles, ovigerous controls from April 15 shipment; C, destalked from February 25 shipment; open circles 10L:14D; solid circles LL; and D, open circles, destalked from January 13 shipment; solid circles, destalked ovigerous from April 15 shipment.

with increasing weights, and no ovaries weighing above 60 mg. This represents a fairly normal J-shaped distribution. The crabs from the January shipment had ovaries in higher weight classes than those attained by ovigers in the April shipment. The distributions for crabs observed throughout the autumn are shown in Table II and are essentially like those illustrated in Figure 2B. The clustering in the smallest weight class was slightly more exaggerated in September, October and November, while in December 100% of the ovaries weighed less than 10 mg.

Three color classes are readily distinguishable on visual examination of the ovaries: purple, the color of mature ova, orange, infrequently present in control crabs, and colorless, characteristic of immature ovaries. The relative frequencies of occurrence of the three color classes for September through May are seen in Table III. It is apparent that the proportion of colorless ovaries in intact crabs is maximal from September through December. The proportion drops in January when the proportion of purple begins to increase. There follow precipitous drops in the proportion of colorless ovaries through March for all crabs and into April for non-ovigers. For those that oviposited in mid-April, the proportion of colorless ovaries abruptly increases. For intact crabs the orange color occurs with maximum frequency (22%) in March and April.

The relative frequencies of molting in intact crabs are shown in Figure 1B. During September and October there were practically no molts, the frequency rose

TABLE II

Distributions for crabs observed throughout the autumn.

Observation dates	9/15 to 10/6		10/28 to 11/27		11/27 to 12/14		12/31 to 1/28	
Weight class (mg)	A	B	A	B	A	B	A	B
130–139.9	0	0	0	0	0	0	4	0
120	0	0	0	0	0	0	4	0
110	0	0	0	0	0	0	0	0
100	0	2	0	0	0	0	4	0
90	0	0	0	0	0	0	4	0
80	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	4	0
60	0	0	0	0	0	0	4	0
50	0	0	0	0	0	0	7	2
40	0	2	0	0	0	0	14	0
30	2	0	11	0	0	0	7	2
20	15	0	18	0	0	0	27	2
10	54	0	37	7	7	0	21	19
0–9.9	29	95	33	92	93	100	4	73

A = destalked crabs; B = intact crabs.

abruptly in November and still further in December, and dropped again during January through April. The ovigers which showed no molts from egg-laying until mid-May, showed a very high frequency of molts during the last half of May. Comparison of Figure 1B with Figure 1A makes it clear that there is a generally negative correlation between ovarian weights and molting frequency. Maximal molting coincides with minimal ovarian weights (December and late May), and there is a very low frequency of molt in March and April when ovarian weights are maximal. However, molting frequency is low in September and October when ovarian weights are also low and again in January when the ovaries are just beginning to show an increase in weight.

TABLE III

Relative frequencies of three color classes of ovaries.

	Controls				Destalked			
	C	O	P	Number of crabs	C	O	P	Number of crabs
September–October	96	0	4	75	4	85	11	67
November–December	95	0	4	56	7	84	9	43
January	74	7	19	42	0	34	66	41
February–March	39	10	51	100	4	54	41	44
March–April	19	22	58	136	12	48	39	66
Ovigers:								
April	75	11	14	45	0	61	39	38
May	86	0	14	14	25	56	19	24

C = colorless; O = orange; P = purple.

Effects of eyestalk removal

The effect of destalking on mean ovarian weights, expressed as differences from the controls, is shown in Figure 3A. Clearly the maximum effect is obtained in January, thus coinciding with very early ovarian maturation. The ovarian weights of destalked crabs are significantly different from those of the controls for September through January and again in April and May for ovigers, as judged by Student's t-test ($P < 0.05$).

In Table I are seen the gonadal indices, variances, and CW for destalked crabs. The CW ranges from 14.6 mm (September and December) to 16.0 mm (January). The gonadal index is higher than that for intact animals in all months and reaches its lowest value in December. The differences between gonadal index of intact and destalked crabs show the same general pattern as that shown by differences in ovarian weights.

Relative frequency distributions by weight classes for destalked crabs are shown in Figure 2C and D. The distributions in Figure 2C are for crabs received February 25. Those in Figure 2D are for crabs received January 13 and for the ovigerous crabs received April 15. Comparison with the control crabs for the same periods (Fig. 2A, B) reveals that following destalking there is a sharp reduction in the proportion of ovaries occupying the smallest weight class. The distributions for September through January are seen in Table II. The initiation of growth in originally immature ovaries is a consistent effect of destalking with variations related only to the proportions of completely immature ovaries found in the controls. The greatest change in distribution is seen in January (Table II) when destalked crabs show a distribution approaching in heterogeneity that seen for intact crabs in February and March.

One of the most conspicuous differences between ovaries of destalked and those of intact crabs is the increase in frequency of orange color in the former. The highest frequency occurs in the post-breeding months when no orange ovaries are found in the controls (Table III). The lowest frequency of orange in destalked crabs is found in January when the greatest weight increase occurs. At this time also the destalked crabs achieved the highest proportions of the purple color that characterizes the mature ovaries of intact crabs. In February and March, while mean ovarian weights still exceeded those of intact crabs, the proportion of purple ovaries actually decreased relative to the controls.

The frequencies of molting in destalked crabs relative to the controls are presented in Figure 3B. Maximum effectiveness in inducing molt occurs in September at a time when molt frequency is low in the controls (Fig. 1B), and again in April and early May for ovigerous crabs when no controls molted. In November, when 34% of the controls molted, there were slightly fewer destalked crabs that molted (27%). In late May both destalked post-ovigerous crabs and their controls molted at a frequency of about 42%.

Although there was no great difference between controls and destalked crabs with respect to survival, there were two times during this study when mortality was high for both groups. One time was in December and the other was in late May. Both are times when controls were undergoing ecdysis during the experimental period. In these cases the deaths occurred in ecdysis or just prior to ecdysis
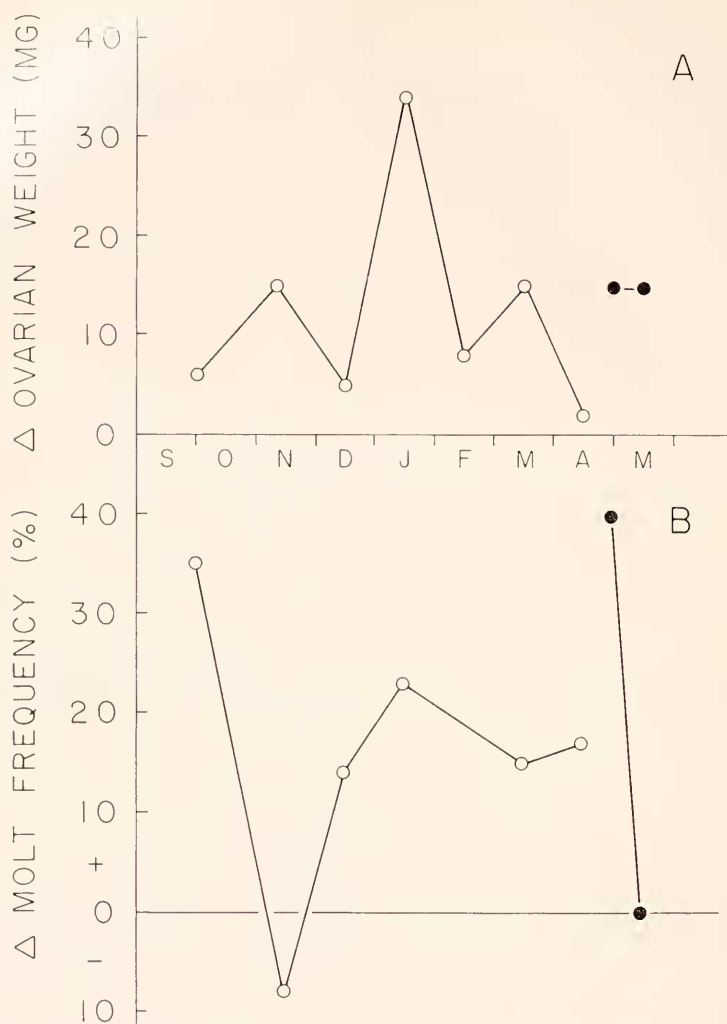
FIGURE 3. A, change in ovarian weights following eyestalk removal, expressed as difference from controls, as a function of time of year; and B, change in molt frequency following eyestalk removal, expressed as difference from controls, as a function of time of year. Open circles represent nonovigers; solid circle, April ovigers.

as revealed by autopsy. During the other times of year ecdysis was generally successful both for destalked and intact crabs.

Egg-laying was infrequent in the laboratory except during the period immediately following April 15. The earliest laying by intact crabs occurred in late March when two crabs laid eggs. For destalked crabs, one crab laid eggs 16 days after destalking in January, and one did so 18 days after destalking in February. Four destalked crabs oviposited in March at intervals of from 20 to 23 days after destalking. It was during this same four-day period that the intact crabs oviposited. No

TABLE IV

Occurrence of molt in experimental periods.

Observation period	Number of molts		First and last day		Median day	
	Experimental	Control	Experimental	Control	Experimental	Control
9/16–10/6	22	1	13–22	19	18	—
10/28–11/27	10	12	9–21	10–17	14	12
11/27–12/14	1	1				
	17*	9*	8–16	8–17	12	10
12/31–1/28	11	2	13–27	16–18	21	16
	5*	0	4–9	—	6	—
2/26–3/29	13	1	16–29	20	22	—
4/15–5/5	12	0	10–20	—	15	—

* Dead in ecdysis or very close to it.

nonovigerous crabs were destalked after April 15. All of the crabs that laid eggs in the laboratory attached the eggs to the pleopods in an apparently normal manner.

DISCUSSION

Throughout the course of this study obvious changes in the condition of the ovaries, in molting frequency, and in the response of crabs to removal of eyestalks were observed. As with any laboratory study, a number of questions can be raised concerning the relevance of the observations to events in the field and the completeness of the sample studied.

For intact crabs, the overall pattern of ovarian conditions is one of decreasing weights from September through December, followed by a gradual increase from January through March, with first egg-laying occurring in mid-April. To what extent can these changes be explained on the basis of systematic differences in the size classes examined? While it is true that the minimal ovarian weight occurs at the time of minimal CW (December), the times of maximal ovarian weights do not correspond with those of maximal CW. A similar lack of correlation between gonadal indices and CW is seen to exist in Table I. It therefore seems that the pattern observed is not attributable to differences in size classes of the samples examined.

To what extent are the observed animals representative of those in the field? The crabs received in September, October and April were freshly collected, while those in December, January and February had been maintained in holding tanks for varying periods. It was seen in Figure 1A that the mean ovarian weights observed for freshly collected crabs that were not carrying eggs agreed well with the weights obtained for crabs received February 26 and observed in March and early April. Since these latter observations were made on crabs that had over-wintered in holding tanks, it seems that the holding conditions permit ovarian development essentially the same as that occurring in the field. The question of whether the samples examined were *completely* representative of the natural population is more involved. The observation of first egg-laying in mid-April agrees with the report of Salmon and Astaides (1968) for this species in the North Carolina area. It is consistent

with the report of Herrnkind (1968) with respect to the beginning of active repro-
duction in Florida. However, the finding in this study that April ovigers molted
before any further ovarian development occurred, as well as the absence of ovigers
and of crabs with mature ovaries in September and October are inconsistent with
Herrnkind's report of practically all females being in berry from May to October.
Such a situation would imply that the crabs mature eggs while carrying one clutch
and oviposit immediately after hatching. While it is possible that in autumn oviger-
ous females were absent from the collection but that some were present in the field,
it is obvious that there were large numbers of nonovigerous females available for
collection. Most of the crabs examined in this study for which the date of oviposi-
tion was known and which were examined within a week or ten days were found
to have a few large purple or orange ova visible in the ovary. Only a very few of
the crabs examined from the September or October shipments showed any evidence
of recent oviposition. Since no observations were made between May 30 and Sep-
tember 15, it is not possible to say whether a molt follows each hatching that occurs
throughout the summer. However, if the crabs received in September had been
ovigerous as late as the end of August, it seems likely that the molt following the last
oviposition of the season is delayed until November or December.

On the basis of the observations presented here, it appears that the active breed-
ing season for crabs in Panacea begins in April and has concluded by mid-Septem-
ber. The crabs that oviposit in April represent about 30% of the population, and
they molt in late May. Another third would be ready to oviposit by early May and
the final third by late May or early June. The presence of ovigers at all times from
April through August could be accounted for by a repetition of the sequence of ovi-
position-hatching-molt with the first ovigers of the season having completed their
second vitellogenesis by mid or late June. Given such a pattern, a compression of
the breeding season could be achieved by increased synchronization of ovarian
maturation together with reduction in the number of times the sequence is repeated.
A factor contributing to synchronization of the first oviposition at the northern
limits of the range for *U. pugilator* might be the restraint placed on early vitel-
logenesis by low temperature.

The significance of the orange color in the ovaries is not clear. The normal
purple color of mature ovaries of this species is that of a caroteno-lipoprotein which
has been partially characterized by Wallace, Walker and Hauschka (1967). Ab-
sorption in the range of visible light is a function of solvent conditions, and the
original purple color is readily changed to orange by a variety of factors, including
pH. The alteration of color need not involve major structural change in the lipopro-
tein. Thus, the appearance of the orange color need not imply change in the syn-
thetic pathway but may simply reflect general metabolic changes induced by eye-
stalk removal. Since the maximum development of the orange color in destalked
crabs occurs when mean ovarian weights are decreasing in the controls, and min-
imally when they begin to increase, it is possible that the differences are related
to varying amounts of ovary-stimulating hormone. For the destalked animals the
relative frequencies of orange and purple in January approximate those seen for
intact crabs in March and early April. January was also the time when the weight
distributions for ovaries of destalked crabs were most different from those of their
controls, and came to resemble the March distributions for intact crabs. Thus, in

January many crabs appeared to undergo a more complete vitellogenesis as a result of destalking than had occurred in the preceding months.

The effectiveness of destalking in inducing molt can be considered in terms of both increased frequency of molt relative to controls and the time required for molt to occur after the operation. Passano (1953) concluded that if molt occurred within ten days after eyestalk removal, the crab was in premolt when the operation was performed and molt could not be attributed to removal of eyestalk MIH. In this study the only experiment in which most of the molts occurred within ten days was that begun May 15, in which post-ovigerous crabs were destalked and 42% of both controls and destalked molted within ten days. In the other two periods when enough controls molted to make a comparison useful (November and December) both controls and experimentals were undergoing ecdysis at approximately the same time (Table IV). In neither of these two months does there seem to have been any effect of destalking so far as molt is concerned. On the other hand, for those months in which destalking did induce molt, there are variations in the time required for molt to occur. The median days of molt for January and March were days 21 and 22 after eyestalk removal, while for late April the median day is day 15. Very few controls molted in any of these months. This suggests that, although MIH is present in intact crabs in all three periods, the crabs destalked in April were closer to molt than were those destalked in January or March.

Summary

1. The condition of the ovaries of intact and eyestalkless *Uca pugilator* from Florida was examined throughout the period from mid-September to the end of May. The frequency of molt for the animals was also observed.

2. Ovarian weights for intact crabs decreased from September to December and began to increase in January. The increase did not occur uniformly throughout the population, and by March all stages of maturation were present. First oviposition occurred in April, involving about 30% of the females. No oviposition occurred as late as mid-September.

3. Crabs that oviposited in April did not exhibit further vitellogenesis prior to molt which occurred in late May. A high frequency of molting again occurred in intact crabs in November and December.

4. Removal of eyestalks led to initiation of vitellogenesis in immature ovaries at all times tested and also appeared to increase the rate of vitellogenesis in already maturing ovaries.

5. Removal of eyestalks increased the frequency of molt maximally in September and late April and caused no increase in November and December or for post-ovigers in late May.

6. The pattern of reproduction and molt for this species in the months studied appears to consist of the following sequence: vitellogenesis-oviposition-incubation-hatching-molt. The breeding season could be extended by repetitions of the sequence or compressed by increasing the degree of synchronization.

LITERATURE CITED

ABRAMOWITZ, R. K., AND A. A. ABRAMOWITZ, 1940. Moulting, growth, and survival after eye-
    stalk removal in *Uca pugilator*. *Biol. Bull.,* **78**: 179–188.
ADIYODI, R. G., 1968. On reproduction and molting in the crab *Paratelphusa hydrodromous*.
    Physiol. Zool., **41**: 204–209.
ADIYODI, K. G., AND R. G. ADIYODI, 1970. Endocrine control of reproduction in decapod crusta-
    cea. *Biol. Rev.,* **45**: 121–165.
ADIYODI, K. G., AND R. G. ADIYODI, 1974. Comparative physiology of reproduction in arthropods.
    Adv. Comp. Physiol. Biochem., **5**: 37–107.
BOMIRSKI, A., AND E. KLEK, 1974. Action of the eyestalk on the ovary in *Rithropanopeus
    harrisii* and *Crangon crangon* (Crustacea: Decapoda). *Mar. Biol.,* **24**: 325–337.
BROWN, F. A., JR. AND G. JONES, 1949. Ovarian inhibition by a sinus-gland principle in the
    fiddler crab. *Biol. Bull.,* **96**: 228–232.
CHEUNG, T. S., 1969. The environmental and hormonal control of growth and reproduction in
    the adult female stone crab, *Menippe mercenaria*. *Biol. Bull.,* **136**: 327–346.
CRANE, J., 1975. *The fiddler crabs of the world, Ocypodidae: Genus Uca*. Princeton University
    Press, Princeton, New Jersey, pp. 504–505 and 441–447.
GOMEZ, R., AND K. K. NAYAR, 1965. Certain endocrine influences in the reproduction of *Para-
    telphusa hydrodromous*. *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere,* **72**: 694–701.
GUYSELMAN, J. B., 1953. An analysis of the molting process in the fiddler crab *Uca pugilator*.
    Biol. Bull., **104**: 115–137.
HERRNKIND, W., 1968. Breeding of adult *Uca pugilator* and mass rearing of the larvae with
    comments on the behavior of the larval and early crab stages. *Crustaceana Suppl.,* **2**:
    214–224.
PASSANO, L. M., 1953. Neurosecretory control of molting in crabs by the X-organ sinus gland
    complex. *Physiol. Comp. Oecol.,* **3**: 155–189.
PASSANO, L. M., 1960. Molting and its control. Pages 473–576 in T. H. Waterman, Ed., *The
    physiology of Crustacea, Volume 1*. Academic Press, New York and London.
RYAN, E. P., 1965. Structure and function of the reproductive system of the crab *Portunus
    sanguinolentus*. II. The female system. Pages 522–544 in *Proceedings of Symposia
    Series 2. Symposium on crustacea, Part II*. Marine Biological Association of India.
SALMON, M., AND S. P. ASTAIDES, 1968. Visual and acoustical signalling during courtship by
    fiddler crabs (Genus *Uca*). *Am. Zool.,* **8**: 623–629.
WALLACE, R. A., S. L. WALKER, AND P. V. HAUSCHKA, 1967. Crustacean lipovitellin. Isola-
    tion and characterization of the major high-density lipoprotein from eggs of decapods.
    Biochemistry, **6**: 1582–1590.